

LOWER CAMBRIAN REEFAL CRYPTIC COMMUNITIES

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ABSTRACT. Phanerozoic reefs were differentiated into distinctive open surface and cryptic communities from their first appearance. During the Lower Cambrian, cryptic communities were surprisingly diverse with small, solitary chambered archaeocyath sponges, calcified cyanobacteria and a microburrowing (?)metazoan being the most ubiquitous and abundant elements. Putative primitive cnidarians, spiculate sponges and various problematica were also common crypt dwellers. Several species of archaeocyath sponge, as well as cribricyaths, the calcified cyanobacteria *Chabakovia* spp. and possibly boring sponges, were obligate cryptobionts.

Lower Cambrian crypts offered a habitat of reduced environmental stress, and they housed a substantial proportion of the total biotic diversity of early reefs. Cryptic communities were composed of solitary, pioneering organisms and displayed no succession. Lower Cambrian crypts were small, short-lived structures compared with most modern reefal crypts, and were sites of extensive syn-sedimentary cementation supporting the conjecture that crypts did not remain open for long before partial or total occlusion. There is ample evidence, however, of a soft-bodied cryptos and of intense competition for space, as organisms commonly form multiple overgrowths or chains of individuals.

On a sub-zonal scale, the vast majority of archaeocyath species appear simultaneously in both open surface and cryptic niches, suggesting that Lower Cambrian crypts did not serve either as 'safe-havens' harbouring formerly open surface inhabitants or as 'brood-pouches' of evolutionary innovation.

ONE of the most striking aspects of modern coralgall reefs is their differentiation into distinctive open surface and cryptic communities (Jackson and Buss 1975; Jackson 1977; Jackson and Winston 1982; Choi and Ginsburg 1983; Choi 1984; Kobluk 1988). Whilst phototrophic organisms dominate on exposed, open surfaces, filter and suspension-feeding organisms flourish within hidden, or cryptic niches. Of these, encrusting sponges and ectoprocts are particularly abundant as they appear to be the best overgrowth competitors (Jackson and Winston 1982), but solitary organisms such as serpulids, foraminiferans and brachiopods are also conspicuous, even though they occupy little space (Jackson 1977).

Any association of aggregating skeletal organisms will form cavities or crypts within its framework, as well as generating abundant debris which present attractive undersurfaces for colonization. Such primary crypts provide relatively well-protected niches shielded from direct exposure to local environmental pressures, such as wave scour, irradiation and predation. Unoccupied substratum is rare in crypts and overgrowths are common, suggesting that, as at the open surface, competition for space is intense. Nutrient supply and oxygen availability (provided by sufficient water flow) are critically important to modern cryptic communities (Kobluk and James 1979; Choi and Ginsburg 1983), with competition for food and competitive networking being the principal determinants which maintain high diversity (Jackson and Buss 1975).

Cryptic niches are extremely important within modern reef ecosystems, as many organisms are far more abundant in crypts than on open surfaces and some may be obligate cryptobionts. Crypts can thus house a significant proportion of the total biotic diversity of a reef. In addition, modern reefal caves and grottoes have attracted a celebrated status for the ancient affinities of their biotas (Jackson *et al.* 1971). These crypts house putative relict communities of Mesozoic reef-building calcified demosponges ('sclerosponges') and thecidioid brachiopods (Jackson *et al.* 1971; Wood 1990). Such large cryptic niches have been suggested to be refugia or 'safe havens' to which once-

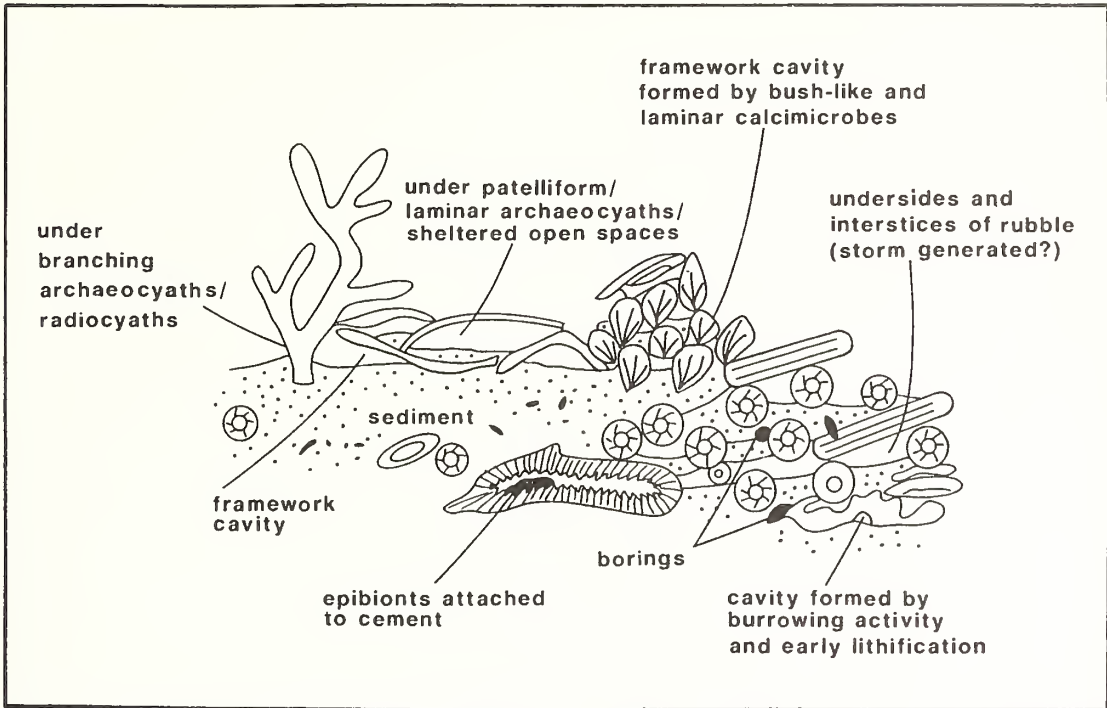
widespread organisms have retreated in the face of new competition (Jackson *et al.* 1971; Vermeij 1985). Others have suggested that crypts may be the crucibles or 'brood-pouches' of evolutionary innovation which spawn new forms that subsequently colonize the open surface (Kobluk and James 1979).

Despite their acknowledged importance in modern reefs, cryptic biotas within fossil reefal buildups have been the subject of limited study (see summaries in Kobluk 1981*b*, 1988). Cryptic communities often go unrecognized in palaeoecological analyses. Although isolated communities have been well documented, it has not yet been established when a distinctive cryptos first developed within reef ecosystems. Nor have any studies been devoted to detailing patterns of temporal development within the cryptos as distinct from open surface communities. Here, we have attempted to describe the cryptos in the earliest known Phanerozoic reefs and to document its development.

The oldest Phanerozoic reefs known are from the 'Nemakit-Daldynian' (= Manykaian; earliest Cambrian; some 544 Ma according to Bowring *et al.* 1993) and were pure calcified cyanobacterial mounds. The first metazoan reefs formed with the appearance of archaeocyath sponges within calcified cyanobacterial communities at the base of the Tommotian (530 Ma; Bowring *et al.* 1993). This consortium was joined later in the Lower Cambrian by other calcified heterotrophs such as radiocyaths and coralomorphs. Lower Cambrian reefal communities usually developed as a series of bioherms in fairly energetic shallow shelf seas (Wood *et al.* 1992*a*), and showed no succession apart from initial stabilization of substrates by the growth of calcified cyanobacteria (Hart 1992) or a consortium of pioneer archaeocyaths and calcified cyanobacteria (Kruse *et al.* in press). Where archaeocyaths were present, bioherms were often dominated by only one or two modular, branching species, implying the rapid colonization and subsequent growth of only a limited number of larval spat falls (Wood *et al.* 1992*a*, 1993). These bioherms were essentially soft-substrate communities, with few massive or encrusting organisms. Early reef communities persisted until the virtual demise of the archaeocyaths at the end of the Toyonian, some 520 Ma (Bowring *et al.* 1993), although calcified cyanobacteria continued to build reefs for the remainder of the Cambrian. Reefs known from the base of the 'Nemakit-Daldynian' to the end of the Toyonian, a period of approximately 25 million years, thus present a coherent ecosystem in which to study the temporal development of cryptic communities.

Crypts are known to have been exploited early in the history of reefs: organic-walled microfossils (*Huroniospera* sp. and *Gunflintia* sp.) and haematitic problematica (*Frutexitis* sp.) have been noted from crypts within lithified algal mat sequences from the Early Proterozoic Odjick Formation, Canada (Hofmann and Grotzinger 1985), and Turner *et al.* (1993) noted *Renalcis*-like cryptobionts in the pre-Vendian Neoproterozoic reefs of the Little Dal Group in northwestern Canada. The first Phanerozoic cryptic communities are documented from the middle Lower Cambrian (Kobluk and James 1979; Kobluk 1981*c*, 1985; Rees *et al.* 1989; James and Gravestock 1990; Fröhler and Bechstädt 1992; Wood *et al.* 1993). These cryptic biotas show, however, marked differences in composition. The cryptos described from the Botomian Poleta Formation in Nevada (Kobluk 1981*a*), the early Toyonian Forteau Formation in Labrador and Newfoundland (Kobluk and James 1979) and the Upper Shady Dolomite in Virginia (Kobluk 1985) have only rare, if any, recorded archaeocyath sponges, even though they have revealed otherwise diverse and unique biotas. In contrast, late Atdabanian cryptic biotas from the Flinders Ranges, South Australia (James and Gravestock 1990) and Zuune Arts, Mongolia (Wood *et al.* 1993) contain abundant archaeocyath sponges, as well as calcified cyanobacteria, putative primitive cnidarians and various problematic forms. Additionally, reported total cryptobiontic diversity and abundance is very variable. These isolated descriptions suggest that cryptic communities were common and well differentiated in Lower Cambrian reefs and deserve systematic study.

Here, we have examined representative reefal communities from throughout the Lower Cambrian. Early cryptic communities were surprisingly well developed, and show biotic and ecological features quite distinct from contemporary open surface communities. We have attempted to highlight these ecological differences by considering differences in morphology and in systematic



TEXT-FIG. 1. Schematic diagram of different cryptic niche types determined within Lower Cambrian reefal buildups.

distribution. In addition, we present quantitative data to test between the competing hypotheses of cryptic niches as 'safe havens' for relict faunas, or as 'brood pouches' of evolutionary innovation.

METHODS

This study is the result of the examination of over 1500 oriented thin-sections from 38 localities embracing 'Nemakit-Daldynian' to middle Toyonian bioherms from the Siberian Platform, South Urals, Altay Sayan Fold Belt, Mongolia, South Australia, Antarctica and North America (see Appendix: Localities 1–38).

We have documented only demonstrably *in situ* elements of the cryptic biota. Although sediment infills within crypts often contain bioclastic debris (such as small shelly fossils, trilobite fragments, brachiopod valves, sponge spicules and echinoderm ossicles), this material is often equally abundant in the non-crypt micrite and interbiohermal sediments of reefal sequences. We have excluded such skeletal material from our analyses except where preferential enrichment within crypts is evident.

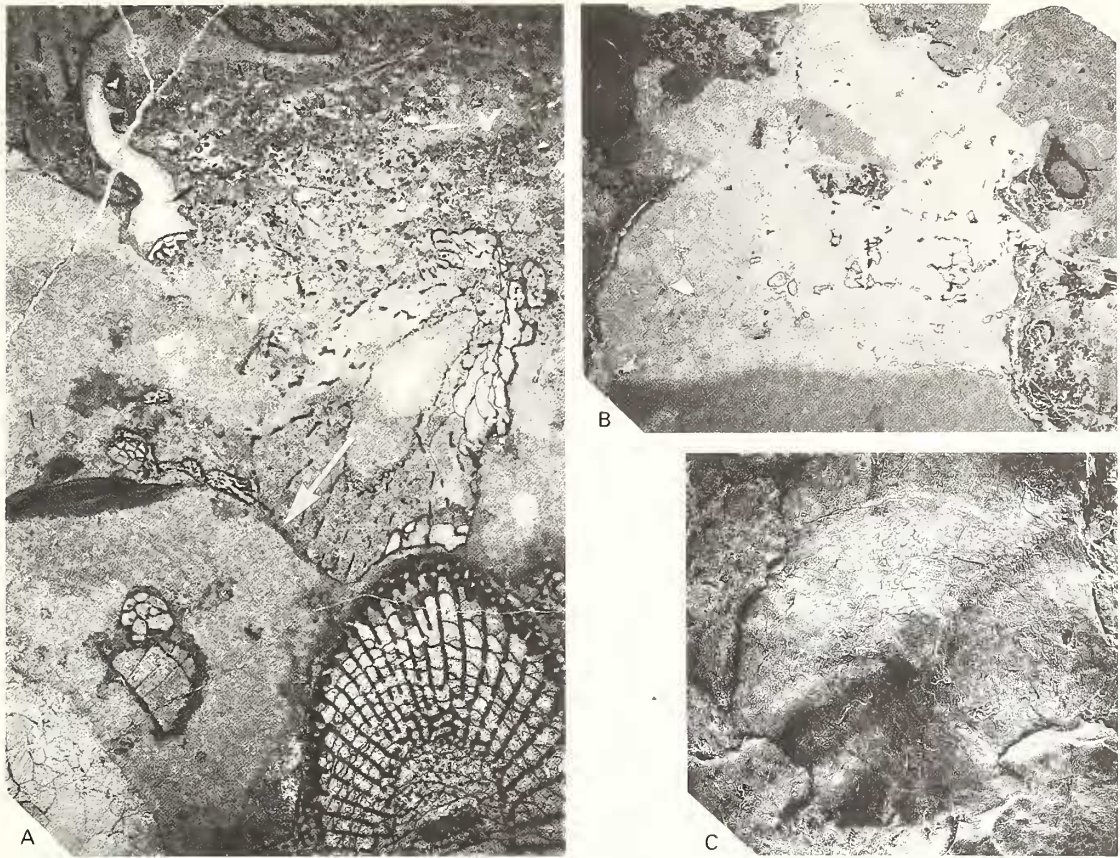
We follow the terminology outlined by Kobluk (1988) and the biostratigraphy of Mansy *et al.* (1993) given in Table 1. Most of the material described herein is housed in the Palaeontological Institute, Russian Academy of Sciences, Moscow (PIN) with supplementary material from the Northern Territory Geological Survey, Darwin, Australia (NTGS), the Sedgwick Museum, Cambridge (SM), and the National Museum of Wales, Cardiff (NMW).

VARIETY AND FORM OF CRYPTS

A surprising variety of cryptic niches was present within Lower Cambrian buildups (Text-fig. 1), whose size ranged from a few millimetres in diameter to several decimetres in some cases. Many

TABLE 1. Biostratigraphy and correlation of Lower Cambrian (Tommotian to Toyonian) in the studied localities studied using archaeocyath zonation (modified from Mansey *et al.* 1993)

Stage	Zone	Siberian Platform	Altay-Sayan	Australia	Mongolia	North America
		Zhuravleva <i>et al.</i> 1969, 1976 (revised)	Osadchaya <i>et al.</i> 1979	Zhuravlev and Gravestock in press	Voronin <i>et al.</i> 1982	Mansy <i>et al.</i> 1993
Toyonian	3		<i>Erbocyathus heterovallum</i> <i>Tegerocyathus edelsteini</i>			
	2	<i>Irinaeyathus shabanovi</i> <i>Archaeocyathus okulitchi</i> Beds	<i>Irinaeyathus ratus</i> <i>Archaeocyathus kusmini</i>	<i>Archaeocyathus abacus</i> Beds		<i>Tegerocyathus greenlandensis</i> <i>Pycnoidocyathus pearylandicus</i> Beds
	1		' <i>Claruscyathus solidus</i> '			<i>Archaeocyathus atlanticus</i> Beds
Botomian	3	Not established	<i>Syringocyathus aspectabilis</i>	<i>Syrinocnema favus</i> Beds		<i>Pycnoidocoscinus serratus</i> <i>Tabulacoccus kordeae</i>
	2		<i>Terycyathellus altaicus</i>		Not established	<i>Claruscoccus fritzi</i> <i>Metacyathellus caribouensis</i>
	1	<i>Rozanovicyathus alexi</i> Beds <i>Carinacyathus squamosus</i> <i>Botomocyathus zelenovi</i>	<i>Clathricoscinus</i>	Not established		<i>Etlunophylthum whitneyi</i> <i>Sekwicyathus nahanneinsis</i>
Ardabanian	4	<i>Fansycyathus lermontovae</i>	<i>Arturocyathus borisovi</i>	<i>Jugalcycyathus tardus</i>	<i>Alataucyathus jaroschevitschi</i> <i>Tabulacyathellus bidzhaensis</i> <i>Pretiosocyathus subtilus</i> Beds	Not established
	3	<i>Nochoroicyathus kokouhni</i>	<i>Nahivkinicyathus cyroflexus</i>	<i>Spirillicyathus tenuis</i> <i>Warriootacyathus wilkawillinensis</i>		
	2	<i>Carinacyathus pinus</i>	<i>Gordonicyathus howelli</i>			
	1	<i>Retecoscinus zegebarti</i>	<i>Nochoroicyathus marinskii</i>			
Tommotian	4	<i>Dokidocyathus lenaicus</i> <i>Tumuliolynthus primigenius</i>				
	3	<i>Dokidocyathus regularis</i>				
	2					
	1	<i>Nochoroicyathus sumnaginicus</i>				



TEXT-FIG. 2. A SM X25956; transversely folded cup of *Pycnoidocyathus latiloculatus* (Hill) with rich cryptic fauna of *Tumuliolynthus irregularis* (Bedford and Bedford) (top), *Archaeopharetra* sp. (centre) and *Metaldetes lairdi* (Hill) (bottom). The development of syngedimentary cement (lower left) has distorted the growth of *Archaeopharetra* sp. (arrowed) and the cement has also served as a substrate for an encrusting *Khasaktia*-like organism and later generations of irregular archaeocyaths; Locality 32 (Botomian 3); $\times 5$. B, NMW 95.2G.1; probable boring excavations of the ceiling of a crypt, showing scalloped edges. The crypt is formed by *Cambrocyathellus ichuranicus*, Zhuravleva and has been subsequently colonized by *Archaeolynthus polaris* (Vologdin) and *Renalcis jacuticus*, Korde; Locality 2 (Tommotian 1); $\times 6$. C, PIN 3848/701; fungal hyphae on the undersurface of *Okulitchicyathus discoformis* (Zhuravleva); Locality 3 (Tommotian 2); $\times 0.3$.

primary growth framework crypts were formed by upright solitary, branching or laminar reef-building organisms, such as archaeocyath sponges (Pl. 1, fig. 1), radiocyaths (Pl. 1, fig. 5), coralomorphs (Pl. 1, fig. 6) and calcified cyanobacteria (Pl. 1, fig. 3). Areas beneath toppled or reworked skeletal debris also provided shelter crypts (Pl. 1, fig. 4). Selective removal of pockets of sediment by currents or storms within accumulations of reefal debris also formed secondary crypts by early lithification of the remaining sediment. Such crypts may have initiated as open burrow systems (Pl. 1, fig. 2). No crevice crypts have been noted, but this may be due their small size and difficulty of recognition. Peculiar sheet-like cracks have, however, been noted within the 'Nemakit-Daldynian' stromatolites of the Chapel Island Formation in southeastern Newfoundland (Myrow and Coniglio 1991).

The lower parts of crypts were often infilled with homogenous or finely laminated micrite, together

with minor amounts of terrigenous material and variable quantities of bioclastic debris. Sediment infills, which may postdate some cement generations, were commonly microburrowed (Pl. 1, figs 1 and 4), and may be layered and graded indicating episodic sedimentation. The upper parts of crypts may be filled with further generations of early and late cements. The presence of a variety of cements indicates that crypts developed in well-oxygenated and agitated conditions (James *et al.* 1976). Early cements were a ubiquitous feature of Lower Cambrian crypts, with microcrystalline and fibrous rimming cements being especially common (Pl. 1, fig. 1; Text-fig. 2A). The *in situ* skeletal cryptobionta was attached to the walls and ceilings of the crypts, and encrusted framebuilders, other cryptobionts or the surfaces of symsedimentary cements (Text-fig. 3).

LOWER CAMBRIAN CRYPTOBIANTS AND THEIR DISTRIBUTION

Sessile cryptos

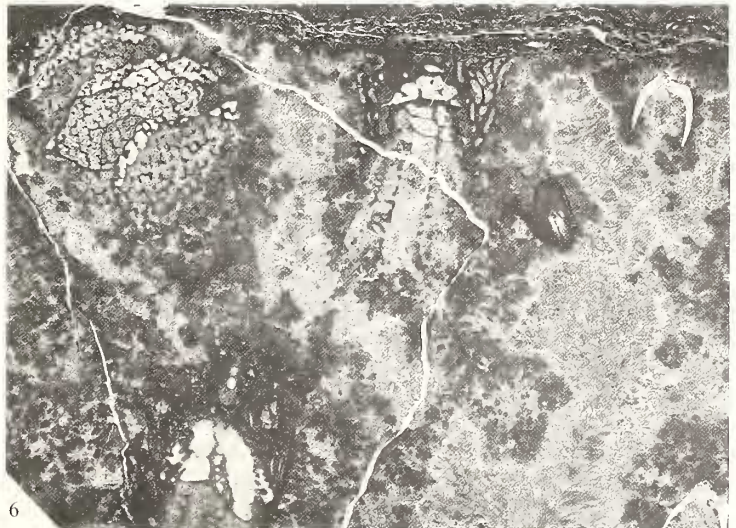
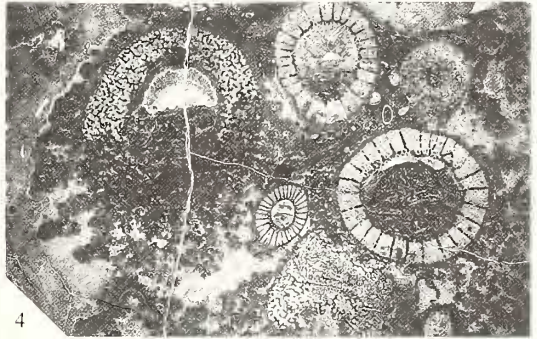
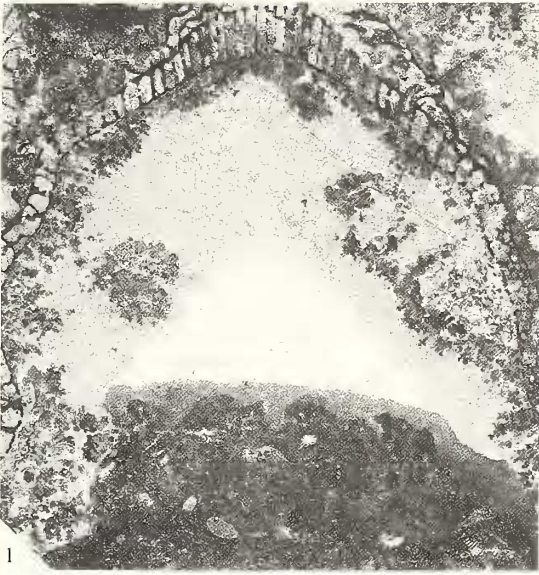
Archaeocyaths. Archaeocyaths were aspiculate calcified sponges, which formed a high-Mg calcite skeleton via calcification of a collagenous template (Zhuravlev 1989; Wood 1990). They were probably closely related to demosponges (Debrenne and Zhuravlev 1992). Archaeocyaths displayed a variety of growth forms although solitary and low integration branching forms were by far the most common (Wood *et al.* 1992a). They appeared at the base of the Tommotian on the Siberian platform, after which they diversified rapidly to reach an acme in the Botomian. During the late Botomian–early Toyonian their diversity plummeted and only two species are known from the post Lower Cambrian (Wood *et al.* 1992b).

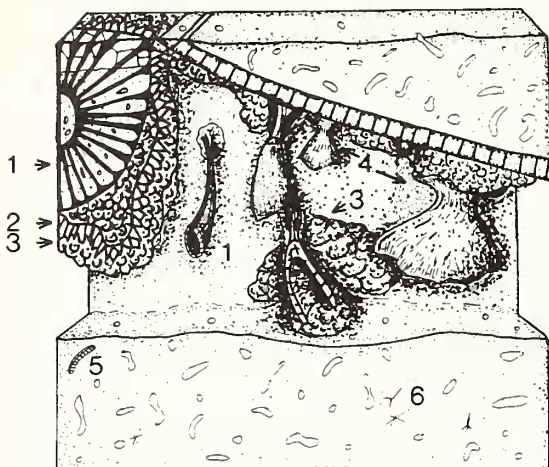
Archaeocyaths were a common to abundant faunal element in Lower Cambrian reefs, forming

EXPLANATION OF PLATE I

Types of Lower Cambrian reefal crypt

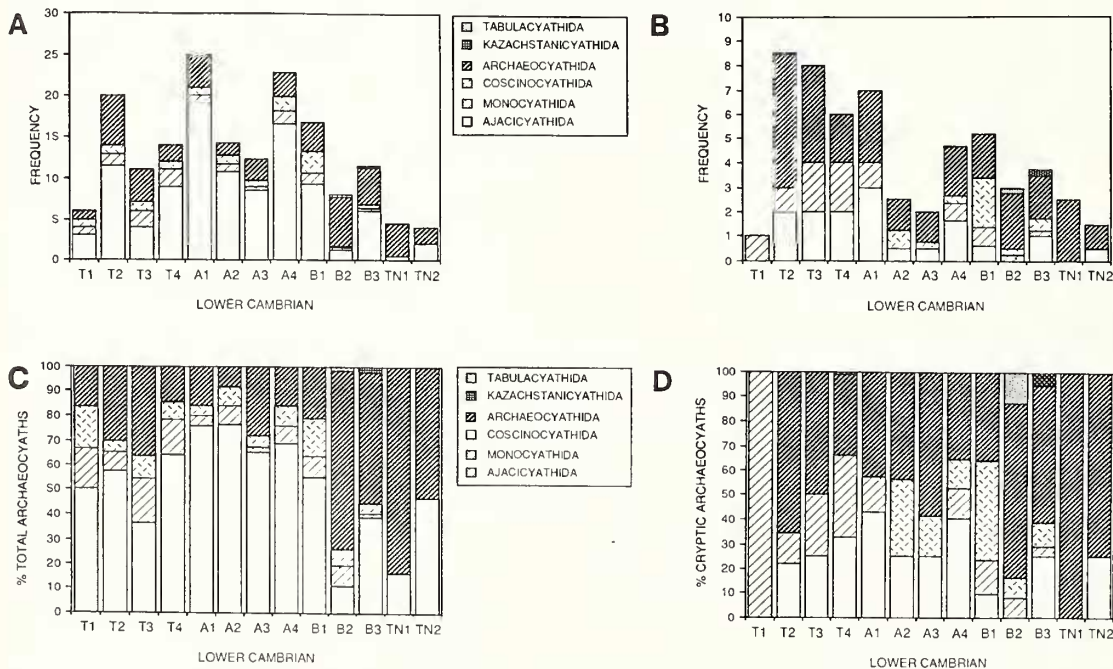
- Fig. 1. NTGS 810028; a domal cup of *Sakhacyathus subatus* (Zhuravleva) forming a crypt colonized by *Renalcis jacuticus* Korde; the first generation of geopetal micrite infill is burrowed and followed by a second layer; all sediment infill postdates *R. jacuticus* encrustation and the precipitation of fibrous calcite; the remaining pore-space is filled with sparry calcite; Locality 3 (Tommotian 2); $\times 5$.
- Fig. 2. NTGS 810038; self-supporting cavity-system formed by symsedimentary lithification of a burrow system, possibly further enhanced by scour; parts of the crypt wall have been colonized by *Renalcis jacuticus* Korde (arrowed); Locality 5 (Tommotian 3); $\times 6$.
- Fig. 3. PIN 4451/90; crypt ceilings formed by rafts of the calcified cyanobacteria *Razumovskia uralica* Vologdin; the resultant crypts were colonized by pendent colonies of *Epiphyton fruticosum* Vologdin and juvenile individuals of the archaeocyath *Spiroclyathella kyzylartauense* Vologdin (arrowed); Locality 25 (Botomian 1); $\times 7$.
- Fig. 4. PIN 3848/702; shelter crypts formed by toppled cups of the archaeocyaths *Dictyocyathus bobrovi* Korshunov (top left), *Nochoroicyathus anabarensis* (Vologdin) (top centre and right) and *Heckericyathus heckeri* (Zhuravleva) (centre); crypts have been colonized by *Renalcis jacuticus* Korde, *Archaeolythus polaris* (Vologdin) (lower centre), and *Dictyocyathus bobrovi* Korshunov; the geopetal micrite infills within the toppled archaeocyath cups have been extensively microburrowed; Locality 7 (Atdabanian 1); $\times 4$.
- Fig. 5. PIN 3482/401; chain of pendent solitary archaeocyath individuals (*Nochoroicyathus changaiensis* (Vologdin) (upper right), *Cambrocyathellus pannonicus* (Fonin) (centre) and *Ajacyathina* gen. et sp. indet. (bottom) forming under the skeleton of the branching radiocyath *Girphanovella georgensis* (Rozanov); several individuals of the cribricyath *Striatocyathus sajanensis* Vologdin and Jankauskas are also present; Locality 19 (Atdabanian 4); $\times 5$.
- Fig. 6. PIN 3848/703; framework crypt formed by the encrusting coralomorph *Khasaktia vesicularis* Sayutina; cryptobionts include pendent archaeocyaths *Neoloculicyathus sibiricus* (Sundukov) (centre and lower left), *Dictyocyathus bobrovi* Korshunov (upper left), the coralomorph *Hydrocoelus* sp. (upper and lower left); this cryptic fauna was subsequently encrusted by the calcified cyanobacterium *Renalcis jacuticus* Korde; Locality 7 (Atdabanian 1); $\times 10$.





TEXT-FIG. 3. Schematic block diagram of a typical Lower Cambrian crypt. 1, archaeocyaths; 2, synsedimentary cements; 3, calcified cyanobacteria; 4, coralomorphs; 5, microburrowing metazoan; 6, bioclastic debris, including sponge spicules.

up to 50 per cent. of the total rock volume of some bioherms. Most were attached by an epitheca to hard substrates, such as calcified cyanobacteria or archaeocyath, radiocyath and coralomorph skeletons. Some large solitary, regular individuals, although initiating upon small ephemeral hard substrates, may have been rooted in lime mud. Many had abundant exocyathoid buttresses which served for both stabilization and binding and as competitive exclusion structures (Brasier 1976; Debrenne and Zhuravlev 1992; Wood *et al.* 1992a). Most irregular forms tend to be in growth



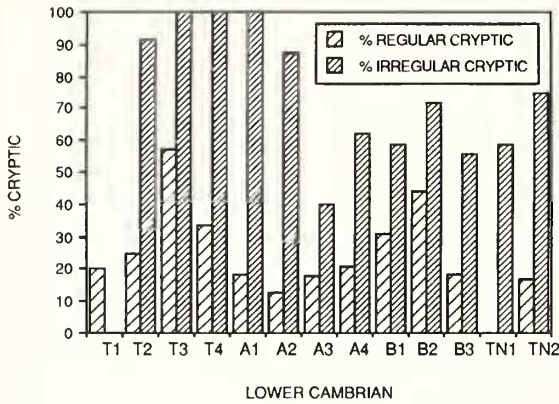
TEXT-FIG. 4. Total number of archaeocyath species within each order in A, total bioherm community, B, cryptic communities only. C, percentage of each order within total communities. D, percentage of each order within cryptic communities only. Community proportions are averaged for each stage.

TABLE 2. Distribution of cryptobionts through the Lower Cambrian. X marks the certain occurrence of cryptic forms. ? marks the probable first appearance. * refer to James and Gravestock (1990) for detailed descriptions.

Cryptobionts	'Nemakit-Daldynian'	Tommotian				Atdabanian				Botomian			Toyonian					
		1	2	3	4	1	2	3	4	1	2	3	1	2	3			
Non-calcified bacteria		<-----																
Calcified cyanobacteria		-----																
<i>Korilophyton</i>	X	----- X																
<i>Angulocehlularia</i>	X	-----																
<i>Botominella</i>		?	-----													X		
<i>Renalcis</i>	X	-----																
<i>Tarthinia</i>	X	-----																
<i>Girvanella</i>	?	-----											X	-----				
<i>Obruchevelia</i>	?	-----												X	-----			
<i>Epiphyton</i>		X	-----															
<i>Tubomorphophyton</i>			?	-----											X	-----		
<i>Gordonophyton</i>			?	-----											X	-----		
<i>Kordephyton</i>			?	-----											X	-----		
<i>Bija</i>		-----											X	-----				
<i>Chabakovia</i>		-----											X	-----				
<i>Wetheredella</i>		-----												X	-----			
'Encrusting microfossils'*		-----											X	-----		X	-----	
'Calcareous microspheres'*		-----											X	-----		X	-----	
Fungi		X-----																
Archaeocyaths:		-----																
<i>Monocyathida</i>	X	-----														X		
<i>Ajaciocyathida</i>	X	-----														X		
<i>Archaeocyathida</i>	X	-----														X		
<i>Kazachstaniocyathida</i>		-----												X	-----			
<i>Coscinocyathida</i>		-----											X	-----		X		
<i>Tabulacyathida</i>		-----											X	-----		X		
<i>Cribricyaths</i>		-----											X	-----		X		
Coralomorphs:		-----																
<i>Cysticyathus</i>		X	---	X	-----											X	-----	
<i>Hydroconus</i>		-----											X	-----		X		
<i>Khasaktia</i>		-----											X	-----		X		
<i>Rackovskia</i>		-----											X	-----				
<i>Aploconus</i>		-----											X	---	X	-----		
<i>Tabulaconus</i>		-----											X	---	X	-----		
<i>Labyrinthus</i>		-----												X	---	X	-----	
Microburrowers	X	-----																
Siliceous sponges	X	-----																
Calcarean sponges		X	-----															
Stenothecoids		-----											?	-----		X	-----	
<i>Archaeotrypa</i>		-----												X	-----			
Pellets		-----											X	-----				
Unidentified borings	X	-----																
Grazers		-----												X	-----			
Microborings		-----											X	-----				

position, where branching individuals were often bound together to form bafflestones and laminar forms bindstones. Reworked archaeocyath skeletal debris was also a common component of interbiohermal sediment.

Contrary to previous accounts (Kobluk and James 1979; Kobluk 1981a, 1985), archaeocyaths were abundant cryptobionts; in most communities studied between 20–60 per cent. of the species represented were cryptic (Text-fig. 4). Monocyathid archaeocyaths appeared as an element in



TEXT-FIG. 5. Percentage of cryptic regular and irregular species as a proportion of the total numbers of regulars and irregulars within individual bioherm communities. Community proportions are averaged for each stage.

cryptic faunas in the Tommotian 1, with regular (Ajacicyathida) and irregular forms (Archaeocyathida) following in the Tommotian 2 (Table 2). Representatives from all six archaeocyathan orders (*sensu* Debrenne and Zhuravlev 1992) were present in crypts, but in markedly different proportions. Irregular archaeocyaths (Archaeocyathida, Kazakhstanicyathida) formed between 7–80 per cent. (averaging approx. 35 per cent.) of the total bioherm community (Text-fig. 4C), yet between 30–100 per cent. (averaging approx. 55 per cent.) of the cryptic community (Text-fig. 4D). A far greater proportion of the irregular order Archaeocyathida and the regular orders Monocyathida and Coscinyathida are represented in any one cryptic community than members of the regular orders Ajacicyathida and Tabulacyathida (Text-fig. 4A–B). During the early Lower Cambrian often all irregular archaeocyaths (archaeocyathids) present in any one community were both open surface and crypt dwellers (Text-fig. 5). Ajacicyathids were only a minor component of the crypts, even though they were the most species-rich order in open surface communities (Text-fig.

TABLE 3. Differences in morphology and abundance between organisms which occur as both open surface inhabitants and cryptobionts.

Biota	Open surface	Crypt
Archaeocyaths	Reef-builders predominantly modular irregulars + large regulars	Small, solitary irregulars and thalimid regulars Abundant exothecal tissue
<i>Renalcis</i> and <i>Epiphyton</i> -groups	Globular, compact	Delicate branching, arborescent
<i>Chabakovia</i>	Absent	Present
<i>Khasaktia</i>	Sheath-like, encrusting	Conical, small attachment site
Microburrowing (?)metazoan	Rare	Abundant
Cribricyaths	Absent	Abundant
Hydroconozoans, <i>Labyrinthus</i> and <i>Rackovskia</i>	Rare	Common
<i>Archaeotrypa</i>	?	Present
<i>Wetheredella</i>	?	Present

4B, D). We have noted only one occurrence of a tabulacyathid: *Putapacyathus regularis* Bedford and Bedford, which occurs in both the open surface and cryptic community (Locality 30; Botomian 3). For all communities where sufficient data is available, the Fisher Exact Test shows statistically significant underrepresentation of ajacicyathids, and significant enrichment of archaeocyathids within crypts at the 5 per cent. level.

The diversity of archaeocyaths within Lower Cambrian cryptic communities was highly variable. Some communities show no cryptic archaeocyaths (localities 12 (Atdabanian 3) and 18 (Atdabanian 4)) whereas others were almost entirely cryptic, e.g. locality 22 (Botomian 1). Here, of the seven cryptic species, five were coscinocyathids (Pl. 2, fig. 5). Although this community has yielded a total fauna of seventeen species, many of these forms were uncommon.

In addition to differences in systematic distribution, cryptic archaeocyaths display distinct morphological differences from those typical of open surface, frame-building communities (Table 3). Firstly, all cryptic archaeocyaths have porous septa. Savarese (1992) argues that such forms were adapted hydrodynamically to low turbulence conditions, which is supported by the fact that modern cryptic niches generally create lower energy settings than the open environment. Secondly, Kobluk and James (1979, p. 203) noted that the rare archaeocyaths found in the lower Toyonian reefs of Labrador (Locality 36) were small and 'poorly organized'. We note too that cryptic forms were often small, but have detected no evidence for any differences in their rate of growth compared with open surface conspecifics. Their small size appears to result from their reduced longevity, i.e. many were young individuals. Most interesting, however, is that those archaeocyath species which possessed both modular and solitary phenotypes, consistently displayed modular forms on open surfaces but solitary organizations in crypts (see Appendix for specific details). The only exception to this is *Cambrocyathellus proximus*, which was present in a modular state in both open surface and cryptic niches within the Tommotian 2 and Tommotian 3 reefs of Siberia. The encrusting, modular species *Altaicyathus notabilis* (Pl. 2, fig. 6), *Dictyofavus araneosus* (Pl. 2, fig. 2) and *Zmyicyathus* sp., however, appear to be obligate cryptobionts together with the chambered, encrusting forms *Polythalamia americana* and *P. perforata* Debrenne and Wood (Pl. 2, fig. 3). When present, these forms were very abundant.

Many cryptic archaeocyaths (both regulars and irregulars) show abundant exothecal tissue (epithecra and buttresses), which was probably necessary to secure firm attachment to the ceiling or walls of a crypt (Pl. 1, fig. 6; Pl. 2, figs 1–2). The pronounced ability to produce abundant exothecal tissue in the orders Monocyathida and Archaeocyathida might thus explain their preferential occupation of crypts.

Archaeocyaths clearly preferred attachment to hard substrates, and pendent chains of individuals have been noted in larger crypts (Pl. 1, fig. 5). Some archaeocyath individuals also show growth in a series of distinct morphological phases, where each phase appears as rapid growth followed by complete cessation (Pl. 3, fig. 4). This might be related to periodic, possibly seasonal, environmental fluctuations.

Calcified cyanobacteria. Calcified cyanobacteria were abundant in many Cambrian platform carbonates, and constructed reefal buildups throughout this period even after the extinction of the majority of archaeocyaths (Rees *et al.* 1989; James and Gravestock 1990; Wood *et al.* 1992a). They were often associated with micrite, and may form a substrate for the attachment of other organisms. James and Gravestock (1990) have suggested that the micrite between *Renalcis* colonies was originally a cement similar to modern sea-floor cements.

Calcified cyanobacteria occurred as framework constructors in the form of substantial upright bushes or rafts, as encrustations around reef dwellers and as pendent colonies in crypts. All forms may have trapped sediment and many were common as facultative cryptobionts (e.g. Pl. 1, figs 1–3). *Renalcis*, *Angulocellularia*, *Chabakovia*, *Gordonophyton* and *Epiiphyton* were especially abundant in crypts, but only *Chabakovia* was a preferential cryptobiont.

Renalcis and *Tarthinia* had a botryoidal external form, consisting of rounded compartments with micritic, fibrous or peloidal walls. Individual colonies are difficult to discern but all these forms

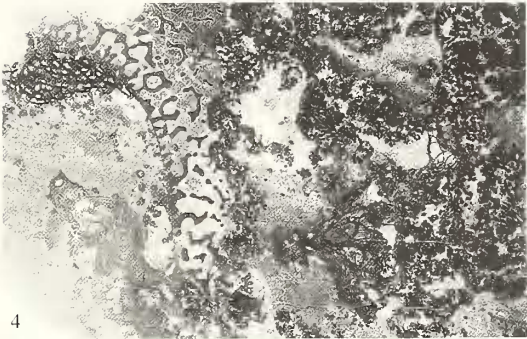
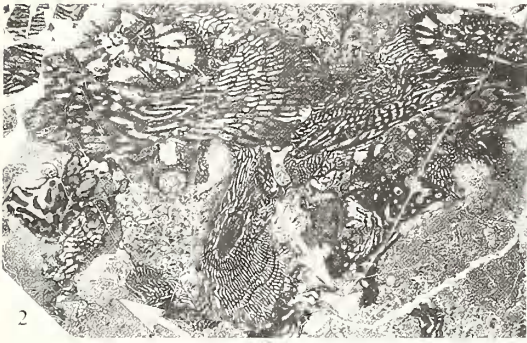
produced dense accumulations or crusts up to 5 mm thick. *Girvanella* formed encrusting sheets or rafts of intertwined microtubules. *Korilophyton*, *Angulocellularia*, *Chabakovia*, *Gordonophyton*, *Epiphyton* and *Tubomorphophyton* all formed dendritic colonies with bifurcating branches and micritic walls. Of these, *Gordonophyton* and *Chabakovia* were the most volumetrically important constituent in crypts (Pl. 2, fig. 4). *Epiphyton*, with short, compact branches (Pl. 1, fig. 3), and *Tubomorphophyton*, with hollow branches, were also common in crypts, whilst *Kordephyton*, which formed branches of radiating fine tubes, inhabited crypts but was generally a relatively uncommon component in Lower Cambrian bioherms.

The previously problematic form *Wetheredella*, noted in the Toyonian reefs of Labrador (Kobluk and James 1979), was suggested by Riding (1991) to be a calcified cyanobacterium. This has been confirmed by the finding of Recent analogues in the mildly alkaline crater lakes of Indonesia, where an identical form grows in crypts and crevices between foliaceous calcified red algae (Kaźmierczak and Kempe 1992). Other Lower Cambrian calcimicrobes noted to be cryptic have probably been misidentified. The calcimicrobe named *Serligia* noted in crypts from the Toyonian of Labrador (Kobluk and James 1979) is probably a fragment of *Botominella*. Likewise, the form *Cavifera* of Kobluk (1985) probably represents a coiled tube of *Obruchevella* sp. The form described by Myrow and Coniglio (1991) as *Frutexitis* sp. is referable to *Angulocellularia*, and was probably a weakly calcified cyanobacterium.

Kobluk and James (1979) noted that *Renalcis* and *Epiphyton*-group calcified cyanobacteria exhibited phenotypy, showing globular and compact morphologies when growing upright on open surfaces, but delicate branches in an arborescent mode in crypts (Table 3). We confirm this observation.

EXPLANATION OF PLATE 2

- Fig. 1. PIN 3848/704; a rich cryptic community within a crypt formed by the calcified cyanobacteria *Renalcis jacuticus* Korde (upper left) and *Epiphyton scapulum* Korde (upper right); the cyanobacterial shrubs have been encrusted by the coralomorph *Khasaktia vesicularis* Sayutina, and the archaeocyaths *Neoloculicyathus sibiricus* (Sundukov), *Dictyocyathus bobrovi* Korshunov, and *Erismacoscinus oymuranensis* A. Zhuravlev; pockets of micrite within the crypt have been extensively microburrowed; Locality 7 (Atdabanian 1); $\times 4$.
- Fig. 2. PIN 4221/51; cavity created by the abundant secondary skeleton of the archaeocyath *Anaptyctocyathus oppositus* (Gravestock) and encrusted by the same species, as well as *Dictyofavus araneosus* (Gravestock) and the calcarean sponge *Dodecaactinella cynodontota* Bengtson and Runnegar (arrowed); these cryptic forms were subsequently engulfed by the secondary skeleton of *A. oppositus*; Locality 14 (Atdabanian 3); $\times 5$.
- Fig. 3. PIN 4451/69; crypt formed under a calcified cyanobacterial colony encrusted by the chambered archaeocyath *Polythalamia perforata* (Vologdin), which was subsequently completely overgrown by *Clathricoscinus popovi* Vlasov; Cryptic *Cribricyathus* sp. is also present (right); Locality 22 (Botomian 1); $\times 10$.
- Fig. 4. PIN 3848/705; crypts formed by the calcified cyanobacterium *Gordonophyton durum* (Korde) encrusted by the archaeocyaths *Dictyocyathus bobrovi* Korshunov, *Ajacyathina* gen. et sp. indet. and the calcified cyanobacterium *Renalcis jacuticus* Korde; Locality 7 (Atdabanian 1); $\times 12$.
- Fig. 5. PIN 4451/91; a cryptic community of the chambered archaeocyaths *Capsulocyathus irregularis* (Zhuravleva), *Tylocyathus bullatus* (Zhuravleva), *Clathricoscinus popovi* Vlasov the cribricyath *Cribricyathus* sp. (top left and bottom right) and the calcified cyanobacterium *Tubomorphophyton* sp.; Locality 22 (Botomian 1); $\times 5$.
- Fig. 6. PIN 4451/92; small crypts within a cyanobacterial bioherm, colonized by tiny individuals of the archaeocyath *Altaicyathus notabilis* Vologdin (arrowed), a weakly calcified coralomorph (lower right), and *Epiphyton* sp. and *Renalcis* sp.; Locality 34 (Botomian 3); $\times 10$.
- Fig. 7. SM X24900; a cryptic individual of the coralomorph *Khasaktia intermedia* Sayutina, with an attached cryptic archaeocyath fauna of small individuals of *Alatacyathus jaroshevitschi* Zhuravleva (left), *Nochorocyathus changaiensis* (Vologdin) (centre) and juvenile cups of *Cambrocyathellus tuberculatus* (Vologdin); Locality 20 (Atdabanian 4); $\times 3$.



Coralomorphs. Early Cambrian calcified putative cnidarians, known as coralomorphs (Jell 1984), are represented by slender, irregular polygonal tubes or open cups and may occur as solitary individuals or small modular colonies (Zhuravlev *et al.* 1993). All forms were encrusting and many had extensive attachment areas.

Of the ten early Cambrian coralomorph genera, at least seven were known from crypts (Table 2). Five were solitary forms (*Cysticyathus*, *Khasaktia*, *Hydrocoonus*, *Aploconus* and *Tabulaconus*), with *Rackovskia* and *Labyrinthus* bearing a modular habit, although the biological affinity of the latter is uncertain (Kobluk 1979). The earliest coralomorph, *Cysticyathus*, was cryptic and appeared in the lower Tommotian. *Hydrocoonus* (appearing in the Tommotian 4), the branching form *Rackovskia* (Atdabanian 4) and *Labyrinthus* (Toyonian 1) were commonly cryptic, whereas *Khasaktia*, *Aploconus* and *Tabulaconus* were both open surface and cryptic dwellers (Pl. 2, fig. 7; Pl. 3, figs 1, 6).

Khasaktia is the only coralomorph to show phenotypy (Table 3). On open surfaces, it forms an extensive encrusting sheet, whereas in crypts it forms a conical, open cup originating from a small attachment site (Pl. 3, fig. 1).

Cribricyaths. Cribricyaths were simple, usually solitary, narrow, conical or horn-shaped calcareous tubes with a bilaterally symmetrical cross-section. Although common in Lower Cambrian reefal sequences they remain largely problematic (Jankauskas 1972). Cribricyaths were obligate and abundant cryptobionts (Pl. 1, fig. 5; Pl. 2, fig. 5), appearing first in the Atdabanian 1 and disappearing from the record in the Toyonian 1 (Table 2).

Siliceous sponges. Siliceous spicules of hexactinellid sponges first appeared in the Tommotian 1. Such spicules were common components of Lower Cambrian reefal sediments, and some crypts appear to be particularly enriched, perhaps representing disaggregated cryptobiontic sponges.

Calcarean sponges. Tor Herm, in the Australian Flinders Ranges (Locality 16; Atdabanian 4) yields an abundant encrusting sponge, described by Reitner (1992) as a pharetronid calcarean named *Gravestockia pharetroniensis*. The skeleton of this sponge, however, consists of triradiate spicules corresponding with the well known Cambrian form *Dodecaactinella*. This form is a common cryptobiont and often grew attached to the holdfast structures of cryptic archaeocyaths (Pl. 2, fig. 2; Pl. 3, fig. 2).

Problematica. Various Lower Cambrian problematica are known only from reefal crypts (Table 2) and many are described from only one locality. These include 'spherical algae' (Kobluk 1985), 'encrusting microfossils' and 'calcareous microspheres' (James and Gravestock 1990), *Archaeotrypa* (Kobluk 1984) and stenotheccoids.

Stenotheccoids became common in bioherms from the early Atdabanian onwards. They were asymmetrical, bivalved organisms with a sinuous alimentary canal, and may represent a separate phylum (Rozov 1984). Most of the brachiopods and brachiopod-like forms noted from Lower Cambrian crypts (Kobluk and James 1979; Kobluk 1985) are stenotheccoids, although brachiopods are indeed also rarely present. The 'globular foraminifera' identified by Kobluk (1985) are probably compartments of *Tarthinia*.

Uncalcified biota. There is evidence for the presence of soft-bodied, encrusting organisms within Lower Cambrian crypts. Distorted areas on the undersurfaces of archaeocyath skeletons are noted, but in the absence of any preserved attached biota (Pl. 3, fig. 3). These areas were subsequently bioimmured by calcified cryptobionts.

In addition, in Locality 19 (Atdabanian 4), cryptobionts are frequently surrounded by an extensive crystalline area which may represent the remains of uncalcified microbial or bacterial encrustations.

Vagrant cryptos

Microburrowing (?)metazoan. Developments of spar-filled tubular or fenestrate fabric which branch at irregular intervals with numerous blind side branches are extremely common within pockets of micrite in Lower Cambrian reefs, especially within crypts (Pl. 1, fig. 4; Pl. 2, fig. 1). The diameter of the tubes is 100–500 μm , and the burrows extend within archaeocyath intervalla and pore-spaces. These forms first appeared in the 'Nemakit-Daldynian' (R. A. Wood and P. D. Kruse, pers. obs.) and continued to be abundant throughout the Lower Cambrian (Table 2).

Similar fabrics have been described from syndeositional crypts in the Lower Cambrian bioherms of the Forteau Formation of Labrador (Kobluk and James 1979), from late Atdabanian buildups of western Mongolia (Wood *et al.* 1993) and from mid-Ordovician bioherms of the Chazy Group of eastern Canada (Pratt 1982; Desrochers and James 1989). Kobluk and James (1979) and Wood *et al.* (1993) suggested them to be the traces of deposit-feeding worms.

The presence of deposit feeders in crypts indicates, as noted by Kobluk and James (1979), that the crypt-infills were soft and that sediment accumulated while the crypts were still able to support life.

Macroburrows. Macroburrows developed in some micrite crypt infills, often beneath the attached cryptos, and may contain pockets packed with consolidated and cylindrical faecal pellets (Pl. 3, fig. 1). These burrows and pellets first appear in the Tommotian 2 (Table 2). Passive stowage of pellets within vacated regions of a burrow system is well known from the Recent and is generally attributed to the activity of infaunal worms (Schafer 1972). *Planolites*, *Torrowangea*, *Teichichnus*, *Paleophycus* and three unidentified traces have also been noted (Kobluk and James 1979) from the crypts of the Toyonian 1 bioherms of Labrador (Locality 36).

Endolithic cryptos

Borers. Kobluk (1981c) and Kobluk and James (1979) noted that although micro- and macroborers were present by the late Lower Cambrian (Toyonian 1), they had not invaded the cryptic habitat. In this study we have found possible evidence of bioerosion in the lowermost Tommotian reefs of Ulakhan-Sulugur (Locality 2). Here, probable borings are present on the walls and ceilings of crypts, and excavate lithified micrite as well as the cryptic biota of *Renaleis jacuticus* and *Archaeolynthus polaris* (Text-fig. 2B). The borings appear to have scalloped edges similar to modern sponge borings, but no excavated chips have been noted. Similar structures have been noted from Atdabanian 2 crypts (Locality 16), where the secondary skeleton of pendent archaeocyaths has been bioeroded (Pl. 3, fig. 5). This style of bioerosion has only been noted in crypts, and was clearly present in metazoan reefs from their inception.

Kobluk (1985) described sinuous microborings (14–20 μm diameter) from the Upper Shady Dolomite, Virginia. These borings show no evidence of branching, reproductive bodies or septation. Similar microborings have been ascribed to the endolithic cyanobacterium *Endoconchia* by Bengtson *et al.* (1990).

Fungi. The first cryptic fungi are noted in the Tommotian 2 (Locality 3), where a dense, cotton-like mass of long, slender, branched tubes (0.3–1.0 mm diameter) covers the undersurfaces of the disc-shaped archaeocyath *Okulitchicyathus discoformis* (Text-fig. 2C). The relatively large size and flattened morphology of these tubes exclude them from being boring bacteria. Their size and distinct septation suggest them to be the hyphae of fungi (ascomycetes or oomycetes).

ECOLOGY OF LOWER CAMBRIAN CRYPTS

Competition for space in Lower Cambrian reefs must have been severe to produce differentiated and distinct open surface and cryptic communities. This is confirmed by the observation that

cryptobionts commonly formed multiple overgrowths or chains of individuals in crypts (Pl. 1, fig. 5; Pl. 2, fig. 1), indicating that much of the crypt surface was covered with both calcified and non-calcified organisms. The small patches of hard substrate provided by pendent archaeocyaths may have been the only areas available for colonization by later generations of cryptobionts.

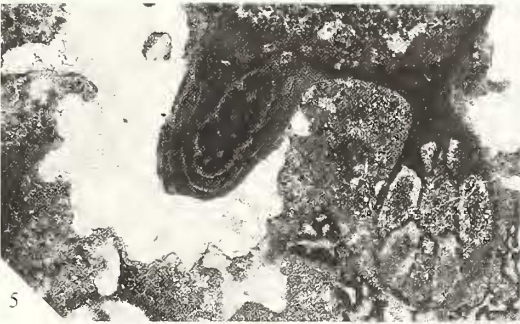
There is also evidence for encrustation of crypt-forming archaeocyaths during their life, as their calcareous skeletons show evidence of distortion in response to attached calcified and non-calcified cryptobionts (Pl. 3, fig. 3). The development of the cryptos was thus contemporary with framebuilder growth, and chains of pendent cryptobionts are also noted to have grown synchronously (Pl. 3, fig. 6).

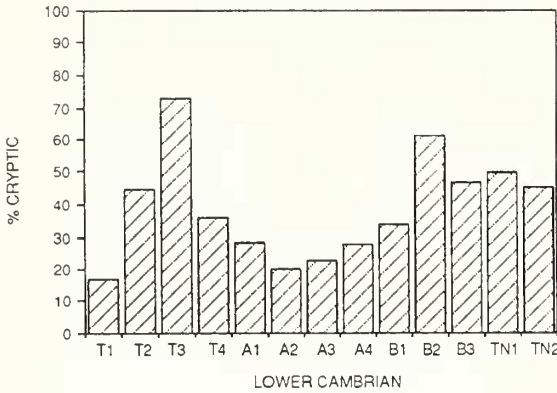
The apparent diversity and abundance of life in any one crypt appears to have been a function of overall community diversity, the size of the crypt and the length of time crypts were available for colonization. The zone-averaged diversity of archaeocyath species within the cryptos through the Lower Cambrian shows a marked decline from the Tommotian 2 onwards (Text-fig. 4B). When analysed, however, as a percentage of total community diversity, no such trend is apparent (Text-fig. 6); crypt diversity, at least as reflected by the richness of the archaeocyath fauna, appears to be broadly a function of overall community diversity.

Yet individual Lower Cambrian communities show a tremendous range of cryptobiont diversity, both within and between different communities. For example, the very dense bioherms formed by the calcified cyanobacterium *Razumovskia* in Eastern Sayan (Localities 11, 12 and 18) possess extremely small cryptic niches, and except for calcified cyanobacteria a cryptic biota was absent in spite of a rich open surface community of 20–45 archaeocyath species. In contrast, the large crypts formed during the mid–late Tommotian of Siberia (localities 3–5) housed a diverse and abundant cryptos. Although this phenomenon is difficult to quantify, large cavities contain more abundant biotas with higher diversities, and also show more examples of multiple overgrowths and chains of individuals (e.g. Pl. 1, fig. 5; Pl. 2, fig. 1).

EXPLANATION OF PLATE 3

- Fig. 1. PIN 3848/706; a secondary crypt formed by a cryptic individual of the coralomorph *Khasaktia vesicularis* Sayutina, which has been colonized by a further individual of the same coralomorph; the crypt was later infilled with micrite, which has subsequently been burrowed; some burrows show the stowage of faecal pellets; Locality 8 (Atdabanian 2); $\times 5$.
- Fig. 2. PIN 4221/52; a cryptic individual of the encrusting calcarean sponge *Dodecaactinella cynodontota* Bengtson and Runnegar forming a further crypt colonized by pendent *Ajacyathina* gen. et sp. indet. (left) and *Archaeocyathina* gen. et sp. indet. (right); the archaeocyath *Metaldetes ferulae* Gravestock and the calcified cyanobacterium *Chabakovia?* sp. are attached to the cup of *Archaeocyathina*; Locality 15 (Atdabanian 3); $\times 7$.
- Fig. 3. PIN 3848/707; distortions caused by the attachment of *Hydroconus* sp. (right) and uncalcified biota (arrowed) to the undersurface of the archaeocyath *Dictyosycon gravis* Zhuravleva; this fauna developed underneath the toppled cup of *Arturocyathus varlamovi* A. Zhuravlev and *Renalcis jacuticus* Korde; Locality 7 (Atdabanian 1); $\times 15$.
- Fig. 4. PIN 3848/708; a succession of cryptic, encrusting archaeocyath individuals *Neolocucyathus sibiricus* (Sundukov), and *Ajacyathina* gen. et sp. indet. (bottom), encrusted by the calcified cyanobacterium *Gordonophyton durum* (Korde) and *Renalcis jacuticus* Korde; Locality 7 (Atdabanian 1); $\times 15$.
- Fig. 5. PIN 4221/53; probable borings with scalloped edges, within a spicule-rich mud-infilled crypt inhabited by the archaeocyaths *Rozanovicoscinus stellatus* Gravestock and *Ajacyathina* gen. et sp. indet.; the boring has excavated both lithified micrite and the secondary skeleton of a pendent archaeocyath; Locality 16 (Atdabanian 4); $\times 12$.
- Fig. 6. PIN 4451/93; interacting cryptic growth of two cups of *Hydroconus* sp. and a solitary individual of the archaeocyath *Locucyathus tolli* Vologdin; Locality 23 (Botomian 1); $\times 5$.
- Fig. 7. PIN 3848/709; abundant individuals of the chambered form *Cellicyathus* sp. within an individual crypt; Locality 33 (Botomian 3); $\times 10$.





TEXT-FIG. 6. The percentage of cryptic species within the total bioherm community through the Lower Cambrian. Community proportions are averaged for each stage.

Although the total diversity of cryptic archaeocyaths may be high for any one community, individual crypts, especially those of limited size, were often dominated by a limited number of species (e.g. Pl. 3, fig. 7). This suggests that, as on open surfaces, crypts were colonized rapidly by a limited number of larval spat falls.

On modern hard substrates, solitary organisms are poor space competitors as they generally have small areas of attachment and lack specific competition mechanisms (Jackson 1977, 1985; Hughes 1989). They appear to be more dependent upon disturbance processes to provide suitable sites for settlement and growth than modular organisms. Small size, rapid growth rates and short generation times favour generalist, opportunist or fugitive life strategies (Jackson 1977). However, many solitary species occur throughout a wide range of modern cryptic habitats, whereas most modular forms, especially the best competitors for space, are more limited in the range of depths and substrates that they occupy (Jackson 1977).

In Jamaica, modern foliaceous coral undersurfaces routinely survive tens to hundreds of years (Hughes and Jackson 1980) and are dominated by dense growths of clonal animals and plants (Jackson 1977; Jackson and Winston, 1982). In contrast, shorter-lived substrates, such as *Pinna* shells, are sparsely colonized by scattered serpulids and bryozoans. Jackson (1985) thus proposed that the ratio of modular to solitary species is a function of substrate longevity and, indeed, studies on community development in modern reefal crypts (e.g. Choi 1984) demonstrate that over time an ecological succession takes place from solitary, generalist forms to modular, encrusting organisms.

No such succession has been noted in Lower Cambrian crypts. Lower Cambrian cryptic systems seem to have been dominated by organisms with solitary organizations, be they archaeocyaths, cribriocyaths or coralomorphs, often together with multiple generations of calcified cyanobacterial colonization. Solitary archaeocyaths, which were out-competed by the larger, branching forms on the open surface, were competitively superior in crypts. Although the modular species *Altaicyathus notabilis*, *Dictyofavus araneosus* and *Zunyicyathus* sp. can be abundant in crypts, they were often engulfed by the extensive growth of the secondary tissue of solitary forms (Pl. 2, fig. 2). Modular soft-bodied forms such as siliceous sponges may, however, have been very important competitors in Lower Cambrian crypts.

The continued dominance of solitary archaeocyaths within crypts throughout the Lower Cambrian is especially noteworthy as modular archaeocyaths became increasingly available during this period (Wood *et al.* 1992a). This, together with the limited number of species present within any one crypt, might suggest that Lower Cambrian crypts were short-lived structures compared with modern reefal crypts, and may have suffered frequent disturbance.

These ecological observations are supported by the fact that cryptobionts are noted to grow against and be distorted by the precipitation of syndimentary cements (Text-fig. 2A). Such cements would have grown rapidly, and would have reduced markedly the size of the cavities as well as leading eventually to the total occlusion of crypt openings.

Although it is difficult to quantify the longevity of individual Lower Cambrian bioherms and their crypts, the small size and dominant solitary to low integration organizations of the framebuilding metazoans (archaeocyaths, radiocyaths and coralomorphs) also suggests that they were relatively short-lived communities (Wood *et al.* 1993). Both Lower Cambrian crypts and their occupants were small compared with modern examples. Modern reef cavities may be vast, and will contain cryptobionts exhibiting a considerable range of sizes. The Lower Cambrian reef ecosystem was thus markedly different from its modern counterpart, with the rapid establishment of an aggregating open surface community of heterotrophs and phototrophs and an attendant cryptos with short generation times, in areas of relative environmental instability (Wood *et al.* 1992a; Wood 1993).

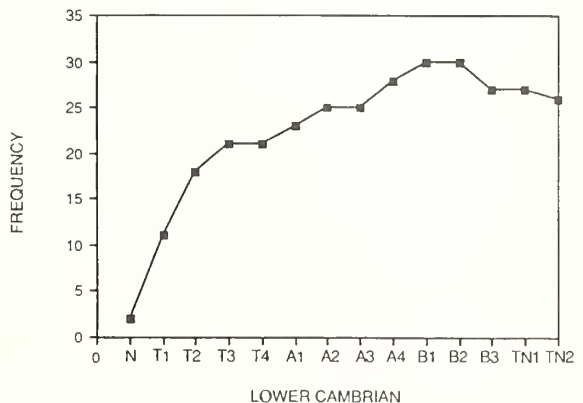
DEVELOPMENT OF THE CRYPTOS THROUGH THE LOWER CAMBRIAN

As predicted by Kobluk and James (1979) cryptobionts were present in the earliest Phanerozoic reefs, in buildups from the 'Nemakit-Daldynian'. In these bioherms, the calcified cyanobacteria *Korilophyton* was present as both upright bushes and as pendent, cryptic colonies. *Angulocellularia* is also known from crypts within stromatolites of this age. Other cryptobiontic calcified cyanobacteria appeared at various times during the Lower Cambrian (Table 2). The first appearance of many of these forms in crypts probably coincides with their first occurrence in the fossil record.

The first probable Phanerozoic cryptic metazoan was a microburrowing organism, which appeared in the 'Nemakit-Daldynian' (R. A. Wood and P. D. Kruse, pers. obs.). Unidentified probable boring organisms and archaeocyath sponges appeared in cryptic niches in the Tommotian 1, and continued to be present throughout the Lower Cambrian (Table 2 and Appendix). All communities studied show irregular archaeocyathids to be proportionally more represented in crypts than regular ajacicyathids (Text-figs 4–5). Phenotypic differentiation occurred in the Tommotian 3–4, when solitary *Archaeolyntus polaris* occupied crypts but a modular phenotype inhabited open surfaces. With the exception of the unidentified borer, obligate cryptobionts did not appear until later in the Lower Cambrian. Cribricyaths appeared in the Atdabanian 1, and obligate cryptic archaeocyaths appeared from the Atbadanian 4 to Botomian 1. All obligate archaeocyaths, including the chambered archaeocyaths, *Polythalamia* spp., possessed encrusting morphologies with large attachment sites.

All large Lower Cambrian cryptic niches were constructed by calcified metazoans, so the appearance of archaeocyaths at the base of the Tommotian vastly increased the size of cryptic niches within reefal buildups. The total diversity of the cryptos follows that of most Lower Cambrian reef-dwelling groups, echoing the general increase in diversity from the Tommotian until the mid-late Botomian mass extinction, and the subsequent decline thereafter (Text-fig. 7). Cribricyaths,

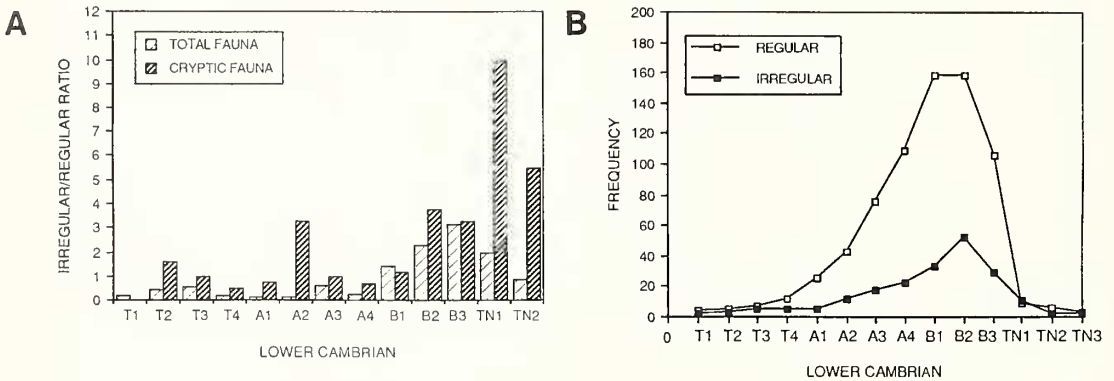
TEXT-FIG. 7. Diversity of cryptobionts through the Lower Cambrian.



together with many coralomorphs (*Khasaktia*, *Hydroconus*, *Rackovskia*, *Aploconus* and *Tabulaconus*) and archaeocyath orders (Monocyathida, Khasachstaniocyathida, Coscinocyathida and Tabulacyathida), were lost during this extinction event, suggesting a major community reorganization after this time. Indeed, only calcified cyanobacteria, together with archaeocyathid and ajacicyathid archaeocyaths survived to populate Toyonian crypts.

As a function of total community diversity, the number of cryptic archaeocyath species is relatively constant through much of the Lower Cambrian (Text-fig. 6), but is noticeably low during the middle-late Toyonian. This might be explained by the increased proportion of large, branching, open surface-dwelling archaeocyaths (Wood *et al.* 1992a) and the reduction of coscinocyathids during this interval. In addition, there was a proliferation of dense *Epiphyton/Gordonophyton* bioherms which did not generally provide large crypts. The Toyonian 1 bioherms of Labrador (Locality 36) were an exception to this, as they were built mainly by *Angulocellularia* and *Renalcis* cyanobacteria. These reefs contained large primary crypts, where a rich cryptobionta with four archaeocyath species has been noted.

Interestingly, the proportion of regular to irregular cryptic species, whilst low for most of the lower Cambrian, increased during the Botomian to reach a peak in Botomian 3 (Text-fig. 8A). This



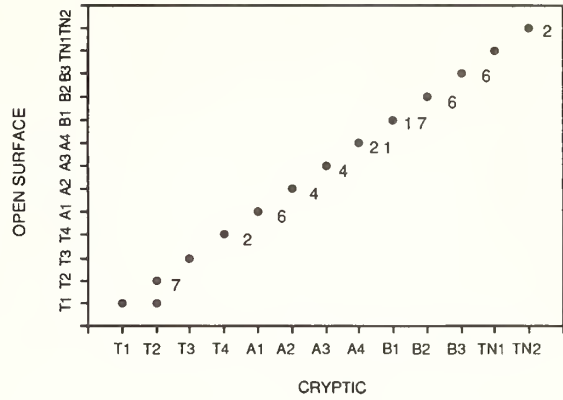
TEXT-FIG. 8. A, Proportion of irregular:regular archaeocyath species present in cryptos of any one bioherm community, through the Lower Cambrian. Community proportions are averaged for each stage. B, Diversity of regulars and irregular archaeocyath genera through the Lower Cambrian (modified from Wood *et al.* 1992a).

reflects the marked increase in global diversity of regulars at that time (Text-fig. 8B). Likewise, the proportion of cryptic irregulars increased markedly in the middle-late Toyonian, following the rapid decline of regulars but continued survival of irregular forms.

TIMING OF CRYPTIC NICHE INVASION

To test the competing hypotheses of cryptic niches as 'safe havens' or 'brood pouches', we have determined the timing to the nearest sub-zone of the first appearance of archaeocyath species in open surface and in cryptic niches (Text-fig. 9). When the first appearance of cryptic species is compared with their first known occurrence, it is clear that, at this temporal resolution, the vast majority of forms appeared simultaneously in both habitats. Many organisms in the Lower

TEXT-FIG. 9. The timing of first appearance of cryptic archaeocyath species on open surface and in cryptic niches. Numbers indicate the number of data points.



Cambrian, however, appeared first in and remained unique to crypts, and there is no evidence of subsequent radiation to the open surface.

If Lower Cambrian reefal communities and hence crypts were short-lived, they offer scant comparison with the long-lived modern reefal caves and grottoes which are known to house organisms up to 1000 years old (Willenz and Hartman 1987). Although few data are yet available, it appears that some of those modern calcified demosponges currently found in crypts have always occupied such niches, and that it is their open surface-dwelling relatives which have been preferentially removed during extinction events (Reitner and Engeser 1987; Wood 1990). There may have been no migration from the open surface to crypts.

Occupation of cryptic niches certainly did not appear to confer preferential survival upon Lower Cambrian cryptobionts. Many common and obligate cryptobiontic metazoans (cribricyaths, some archaeocyaths, and many coralomorphs) perished during the Botomian extinction event (Table 2).

DISCUSSION

The Lower Cambrian reefal cryptos was well developed, and contained a diverse and distinct biota. Apart from a surprising number of obligate cryptobionts (e.g. *Chabakovia*, cribricyaths, some archaeocyaths, infaunal worms and various problematica), one of the most species-rich Lower Cambrian groups, the Archaeocyatha, differentiated early in its history into systematically and ecologically distinctive open surface and cryptic communities. Whilst open surface framebuilders were predominantly branching, irregular forms (Wood *et al.* 1992a), small, solitary irregular archaeocyaths and regulars with chambered (thalamid) organizations were abundant cryptobionts. Like modular forms, only archaeocyaths with porous septa occurred as cryptobionts. Competition for space was intense in Lower Cambrian reefal ecosystems, and crypts housed much of the total reefal diversity.

Cryptic niches offered an alternative habitat of reduced environmental stress. Irradiation and predation do not appear to have been important factors in the Cambrian as they are in Recent reefal crypts. Calcified cyanobacteria were equally abundant in both open surface and cryptic niches, and likewise, except for boring, no evidence of predation of the calcified benthos has been noted in Lower Cambrian reef ecosystems. Reduced hydrodynamic energy would also appear to have characterized the Lower Cambrian crypt.

Lower Cambrian reefs were probably short-lived communities which had little inherent stability without extensive early lithification (Wood *et al.* 1993). The volume of cryptic surface area was variable in Lower Cambrian reefs, and was determined by the individual size of the dominant framebuilders. The size of framebuilders not only determined the size of the crypts, but also the

length of time the crypts were available for colonization; large, relatively stable and long-lived calcified metazoans such as radiocyaths display noticeably more diverse and abundant cryptic biotas than niches formed under small, more fragile forms. Lower Cambrian crypts and their occupants, however, were far smaller than modern examples.

The short-lived nature of many Lower Cambrian crypts compared with modern reefs may explain the dominance of a fauna where solitary organizations were favoured, with often a limited number of species within individual crypts. The rapid growth of synsedimentary cements in crypts may have further reduced the time available for both colonization and growth of the cryptos. Crypts are dominated by rapidly establishing organisms, often with small attachment areas. Solitary forms dominated throughout the Lower Cambrian, which is especially noteworthy within the Archaeocyatha as modular forms became increasingly available (Wood *et al.* 1992a). Forms with encrusting bases appeared in the mid-Lower Cambrian, and several are noted to be obligate cryptobionts.

Chambered sponges appear to have inhabited commonly a cryptic niche through the Palaeozoic. We note that Ordovician sphinctozoans from Koryakia in Russia, and some Silurian aphrosalpingids (which resemble chambered archaeocyaths) from Alaska and the Urals, were common cryptobionts. In addition, Permian sphinctozoans from the Capitan Reef, Texas and New Mexico occupied more commonly cryptic niches than open surface habitats (Wood *et al.* 1994). This hints that several groups of Palaeozoic chambered calcified sponges, previously interpreted as erect reef framebuilders, may in fact have been preferential cryptic dwellers for much of their long history. Chambered calcified sponges exhibit predominantly solitary and low integration, branching morphologies with small attachment sites. Such organizations conferred better competitive abilities within crypts than on open surfaces, where they would have been out-competed by high integration, encrusting organisms with an ability to occupy and cover rapidly new substrate.

CONCLUSIONS

1. Lower Cambrian reefal cryptic communities were surprisingly diverse with archaeocyath sponges, calcified cyanobacteria and a microburrowing (?)metazoan being the most ubiquitous and abundant elements. Putative primitive cnidarians, spiculate sponges and various problematica were also common crypt dwellers.
2. Archaeocyaths differentiated in the late Tommotian into distinct open surface and crypt dwellers. Open surfaces were dominated by solitary ajacicyathids and irregulars with modular, branching organizations, crypts preferentially housed solitary irregulars (archaeocyathids) and solitary chambered forms (coscinocyathids and kazachstanicyathids).
3. *Zunyicyathus* sp., *Dictyofavus* spp., *Altaicyathus notabilis*, *Polythalamia americana* and *P. perforata* were obligate cryptobionts, as were the calcified cyanobacteria *Chabakovia* spp. and all cribricyaths. Infaunal deposit-feeding (?)worms and probable borings, possibly made by sponges, have also been noted only in crypts and were present in metazoan reefs from their inception.
4. Lower Cambrian crypts housed a substantial proportion of the total biotic diversity of early reefs. Cryptic communities were composed of solitary, pioneering organisms and unlike modern reefs displayed no evidence of succession. This may be a result of the small size and short-lived nature of both the crypts and their occupants. Lower Cambrian crypts were the sites of extensive synsedimentary cementation, supporting the conjecture that crypts did not remain open for long before partial or total occlusion. Small, solitary archaeocyaths dominated crypts throughout the Lower Cambrian, even though modular forms became increasingly available during this period.
5. There is ample evidence of a soft-bodied cryptos and of intense competition for space, as organisms commonly form multiple overgrowths or chains of individuals.
6. On a sub-zone scale, the vast majority of archaeocyath species appeared simultaneously in both open surface and cryptic niches, suggesting that Lower Cambrian crypts did not serve either as 'safe havens' harbouring formerly open surface inhabitants or as 'brood pouches' of evolutionary innovation.

7. Several groups of Palaeozoic chambered calcified sponges, previously interpreted as erect reef framebuilders, may in fact have been preferential cryptic dwellers for much of their long history.

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APPENDIX

Lower Cambrian reef communities studied, together with a listing of those archaeocyath species which appear in cryptic niches. The timing of their first appearance in the geological record is given: T: Tommotian; A: Atdabanian; B: Botomian; TN: Toyonian. Forms which are modular on the open surface and solitary in crypts are indicated by S, those which are modular in both niches are indicated by M, and those which bear only a modular phenotype are followed by MM. Obligate cryptobionts are shown in bold. (Aj): Ajacicyathida; (M): Monocyathida; (C): Coscinocyathida; (Ar): Archaeocyathida; (K): Kazachstaniyathida; (T): Tabulacyathida.

- | | |
|---|---|
| 1. Nemakit-Daldyn, Siberian Platform, Russia.
Age: Manykaian
no archaeocyaths | Age: T1, <i>sumnaginicus</i> Zone
T1 <i>Archaeolynthus polaris</i> (Vologdin) (M) |
| 2. Ulakhan-Sulugur, middle Aldan River, Siberian Platform, Russia. | 3. Titirikteekh Creek, middle Lena River, Siberian Platform, Russia.
Age: T2, <i>regularis</i> Zone, lower subzone |

- T1 *Cambrocyathellus tchuranicus* Zhuravleva S (Ar)
 T1 *Archaeolynthus polaris* (Vologdin) (M)
Nochoroicyathus spp. (2) (Aj)
 T2 *Cambrocyathellus proximus* (Fonin) M (Ar)
 T2 *Sakhacyathus subartus* (Zhuravleva) S (Ar)
 T2 *Dictyocyathus translucidus* Zhuravleva S (Ar)
 T2 *Spinocyathus maslemikova* Zhuravleva S (Ar)
4. Zhurinsky Mys, middle Lena River, Siberian Platform, Russia.
 Age: T2, *regularis* Zone, lower subzone
 T1 *Cambrocyathellus tchuranicus* Zhuravleva S (Ar)
 T1 *Archaeolynthus polaris* (Vologdin) S (M)
 T2 *Nochoroicyathus aldanicus* Zhuravleva (Aj)
Nochoroicyathus sp. (Aj)
 T2 *Rotundocyathus spinosus* (Zhuravleva) (Aj)
 T2 *Cambrocyathellus proximus* (Fonin) M (Ar)
 T2 *Sakhacyathus subartus* (Zhuravleva) S (Ar)
 T2 *Dictyocyathus translucidus* Zhuravleva S (Ar)
 T2 *Spinocyathus maslennikovae* Zhuravleva S (Ar)
 T2 *Okulitchicyathus discoformis* (Zhuravleva) (Ar)
5. Byd'yangaya Creek, middle Lena River, Siberian Platform, Russia.
 Age: T3, *regularis* Zone, upper subzone
 T1 *Cambrocyathellus tchuranicus* Zhuravleva S (Ar)
 T1 *Archaeolynthus polaris* (Vologdin) (M)
 T3 *Tumuliolynthus primigenius* Zhuravleva (M)
Nochoroicyathus sp. (Aj)
 T2 *Rotundocyathus spinosus* (Zhuravleva) (Ar)
 T2 *Sakhacyathus subartus* (Zhuravleva) S (Ar)
 T2 *Okulitchicyathus discoformis* (Zhuravleva) (Ar)
 T2 *Dictyocyathus translucidus* Zhuravleva S (Ar)
6. Byd'yangaya Creek, middle Lena River, Siberian Platform, Russia.
 Age: T4, *lenaicus-primigenius* Zone
 T1 *Archaeolynthus polaris* (Vologdin) (M)
 T3 *Tumuliolynthus primigenius* Zhuravleva (M)
 T4 *Nochoroicyathus mirabilis* Zhuravleva (Aj)
 T4 *Nochoroicyathus ridiculus* Rozanov (Aj)
 T2 *Okulitchicyathus discoformis* (Zhuravleva) (Ar)
 T2 *Dictyocyathus translucidus* Zhuravleva S (Ar)
7. Oymuran village, middle Lena River, Siberian Platform, Russia.
 Age: A1, *zegebarti* Zone
 T1 *Archaeolynthus polaris* (Vologdin) (M)
 A1 *Nochoroicyathus anabarensis* (Vologdin) (Aj)
- A1 *Rotundocyathus biohermicus* (Zhuravleva) (Aj)
 A1 *Erisnacoscinus oymuranensis* A. Zhuravlev (Aj)
 A1 *Dictyocyathus bobrovi* Korshunov S (Ar)
 A1 *Dictyosycon gravis* Zhuravleva (Ar)
 A1 *Neoloculicyathus sibiricus* (Sundukov) (Ar)
8. Zhurinsky Mys, middle Lena River, Siberian Platform, Russia.
 Age: A2, *pinus* Zone
 A1 *Dictyocyathus bobrovi* Korshunov S (Ar)
 A1 *Neoloculicyathus sibiricus* (Sundukov) (Ar)
9. Achchagy-Kyyry-Taas, middle Lena River, Siberian Platform, Russia.
 Age: A2, *pinus* Zone
 A2 *Geocyathus latini* (Zhuravleva) (Aj)
 A2 *Coscinoicyathus isointervallumus* Zhuravleva (C)
10. Achchagy-Tuoydakh, middle Lena River, Siberian Platform, Russia.
 Age: A2, *pinus* Zone
 A2 *Fansyicyathus lemontovae* Korshunov and Rozanov (Aj)
 A2 *Coscinoicyathus isointervallumus* Zhuravleva (C)
11. Bazaikha River, Eastern Sayan, Russia.
 Age: A2, *howelli* Zone
Neoloculicyathus sp. (Ar)
Dictyocyathus sp. (Ar)
Archaeopharetra sp. (Ar)
Capsulocyathus sp. (C)
12. Bazaikha River, Eastern Sayan, Russia.
 Age: A3, *cyroflexus* Zone
 no archaeocyaths
13. Bachyk Creek, middle Lena River, Siberian Platform, Russia.
 Age: A3, *kokoulini* Zone
 A2 *Geocyathus latini* (Zhuravleva) (Aj)
 A2 *Coscinoicyathus isointervallumus* Zhuravleva (C)
14. Horse Gully, Yorke Peninsula, Australia.
 Age: A3, *tenius* Zone
 A3 *Anaptyctocyathus oppositus* (Gravestock) (Ar)
 A3 *Dictyofavus araneosus* Gravestock MM (Ar)
15. Section G, Wilkavillina Gorge, Flinders Ranges, Australia.
 Age: A3, *tenius* Zone
 A3 *Dictyofavus araneosus* (Gravestock) MM (Ar)

- A3 *Metaldetes fernlae* Gravestock S (Ar)
Ajacicryathida gen. and sp. indet. (Aj)
Archaeocyathida gen. and sp. indet. (Ar)
16. Tor Herm, Section N, Mount Scott Range, Australia.
Age: A4, *tardus* Zone
A4 *Metaldetes gracilis* Gravestock S (Ar)
A4 *Ergatocyathus tatei* Gravestock (Aj)
A4 *Gordonicyathus levis* Gravestock (Aj)
A4 *Rozanovicoscinus stellatus* Gravestock (Aj)
A4 *Okulitchicyathus ?amplis* (Gravestock) (Aj)
17. Bachyk Creek, middle Lena River, Siberian Platform, Russia.
Age: A4, *lemontovae* Zone
A3 *Geocyathus latini* (Zhuravleva) (Aj)
A4 *Coscinoocyathus marocanoides* Zhuravleva (C)
18. Bazaikha River, Eastern Sayan, Russia.
Age: A4, *borisovi* Zone
no archaeocyaths
19. Zuune Arts Mount, Tsagaan Olom Depression, Mongolia.
Age: A4, *jaroshevitschi-bidzhaensis-subtilis* Beds
A4 *Nochoroicyathus changaiensis* (Vologdin) (Aj)
A4 *Rotundocyathus levigatus* (Vologdin) (Aj)
A4 *Cambrocyathellus tuberculatus* (Vologdin) S (Ar)
A4 *Cambrocyathellus pannonicus* (Fonin) S (Ar)
Okulitchicyathus sp. (Ar)
Archaeopharetra sp. S (Ar)
20. Salaany Gol, Tsagaan Olom Depression, Mongolia.
Age: A4, *jaroshevitschi-bidzhaensis-subtilis* Beds
A4 *Archaeolynthus solidimurus* (Vologdin) (M)
A4 *Nochoroicyathus changaiensis* (Vologdin) (Aj)
A4 *Nochoroicyathus howelli* (Vologdin) (Aj)
A4 *Cambrocyathellus tuberculatus* (Vologdin) M (Ar)
A4 *Cambrocyathellus pannonicus* (Fonin) S (Ar)
A4 *Archaeopharetra marginata* (Fonin) S (Ar)
A4 *Tabulacyathellus bidzhaensis* Missarzhevsky (Ar)
A4 *Alatacyathus jaroshevitchi* Zhuravleva (C)
A4 *Chouberticyathus lepidus* (Fonin) S (Ar)
A4 *Tumuliolynthus karakolensis* Zhuravleva (M)
21. Sukhie Solontsi Valley, Azyrtal Ridge, Kuznetsky Alatau, Russia.
Age: A4, *borisovi* Zone
A4 *Archaeolynthus aequiporosus* (Vologdin) (M)
A4 *Erismaoscinnus* sp. (Aj)
A4 *Tumuliolynthus antiquus* (Vologdin) (Ar)
- A4 *Tabulacyathellus bidzhaensis* Missarzhevsky (M)
A4 *Nochoroicyathus certus* (Voronin) (C)
22. Sukhie Solontsi Valley, Azyrtal Ridge, Kuznetsky Alatau, Russia.
Age: B1, *Clathricoscinus* Zone
B1 *Capsulocyathus irregularis* (Zhuravleva) (C)
B1 *Clathricoscinus popovi* Vlasov (C)
B1 *Polythalamia perforata* (Vologdin) (C)
Coscinoocyathus sp. (C)
B1 *Loculicyathus tolli* Vologdin (Ar)
B1 *Archaeolynthus cipis* (Vologdin) (M)
B1 *Tylocyathus bullatus* (Zhuravleva) (C)
23. Bazaikha River, Eastern Sayan, Russia.
Age: B1, *Clathricoscinus* Zone
B1 *Capsulocyathus subcallosus* Zhuravleva (C)
B1 *Loculicyathus tolli* Vologdin (Ar)
24. Seer'Nuur Lake, Ozernaya Province, Mongolia.
Age: B2, (2038–2043)
B1 *Archaeolynthus solidimurus* (Vologdin) (M)
B1 *Capsulocyathus subcallosus* Zhuravleva (C)
B1 *Clathricoscinus dentatus* (Vologdin) (C)
Archaeopharetra? sp. (Ar)
25. Kuragan-Sakmara Province, South Urals, Russia.
Age: B1
Tumuliolynthus sp. (M)
Dokidocyathus sp. (Aj)
Chouberticyathus sp. (Ar)
B1 *Erismaoscinnus bedfordi* (Vologdin) (Aj)
B1 *Capsulocyathus nalivkini* (Vologdin) (C)
B1 *Spirocyathella kyzylartauense* Vologdin (Ar)
26. Section 24b, Mackenzie Mountains, Canada.
Age: B1, *whitneyi-nahanniensis* Zone
B1 *Robertiolynthus handfieldi* A. Zhuravlev (M)
B1 *Sekwicyathus nahanniensis* Handfield (Aj)
B1 *Acanthopyrgus yukonesis* Handfield (C)
B1 *Protopharetra jimensis* A. Zhuravlev S (Ar)
B1 *Fenestrocyathus complexus* Handfield (Ar)
B1 *Archaeosycon pustulatus* (Debrenne and Gangloff) S (Ar)
Zunyicyathus? sp. MM (Ar)
27. Section 24b, Mackenzie Mountains, Canada.
Age: B2, *fritzi-caribouensis* Zone
B2 *Clarusoscinnus fritzi* (Handfield) S (Ar)
B2 *Markocyathus clementensis* Debrenne (Ar)
Zunyicyathus? sp. MM (Ar)
B2 *Archaeocyathus arborensis* Okulitch S (Ar)
28. GSC 91690, Mackenzie Mountains, Canada.
Age: B2, *fritzi-caribouensis* Zone
B1 *Robertiolynthus handfieldi* A. Zhuravlev (M)

- B1 *Fenestrocycyathus complexus* Handfield (Ar)
 B2 *Clathricoscinus fritzi* (Handfield) S (Ar)
29. Nevada, USA.
 Age: B2, *fritzi-caribouensis* Zone
 B2 *Keriocycyathus arachnais* Debrenne and Gangloff (Ar)
 B2 *Arrhythmocricus macdamensis* (Handfield) S (Ar)
 B2 *Polythalamia americana* Debrenne and Wood (C)
30. Wirrealpa Mine, Flinders Range, Australia.
 Age: B2
 B2 *Putapacyathus regularis* Bedford and Bedford (T)
 B2 *Metaldetes retesepta* (Taylor) S (Ar)
31. Section 25/7, Mackenzie Mountains, Canada.
 Age: B3, *serratus-kordeae* Zone
 B3 *Plicocycyathus rozanovi* (Handfield) (Aj)
 B3 *Protopharetra junensis* A. Zhuravlev S (Ar)
32. King George Island, Antarctica.
 Age: B3, *favus* Beds
 B3 *Tumuliolythus irregularis* (Bedford and Bedford) (M)
Dokidocycyathus sp. (Aj)
Ladaecycyathus sp. (Aj)
 B3 *Bractocycyathus labiosus* Kruse (Aj)
 B3 *Metaldetes lairdi* (Hill) S (Ar)
 B3 *Kruseicnema gracilis* (Gordon) (Ar)
33. Olekma River, Siberian Platform, Russia.
 Age: B3
Cellicyathus sp. nov. S (Ar)
Archaeocycyathus sp. S (Ar)
34. Sanashtykgol Creek, Western Sayan, Russia.
 Age: B3
 B1 *Polythalamia perforata* (C)
 B3 *Clathricoscinus spatiosus* (Vologdin) (C)
Loculicyathus sp. (Ar)
Molybdocycyathus sp. S (Ar)
 B3 *Altaicyathus notabilis* Vologdin MM (K)
35. Ynyrga River, Mountain Altay, Russia.
 Age: TN1, '*Claruscycyathus solidus*' Zone
 TN1 *Archaeocycyathus cumfundus* (Vologdin) S (Ar)
36. L'Anse au Loupe, Labrador, Canada.
 Age: TN1, *Archaeocycyathus atlanticus* Zone
 TN1 *Metaldetes profundus* (Billings) S (Ar)
 TN1 *Archaeosycon billingsi* (Walcott) S (Ar)
 TN1 *Arrhythmocricus kobluki* Debrenne and James (Ar)
 TN1 *Archaeocycyathus atlanticus* Billings S (Ar)
37. Sukhie Solontsy Valley, Azyrtal Ridge, Kuznetsky Alatau, Russia.
 Age: TN2, *ratus-kusmini* Zone
 TN2 *Tegerocycyathus edelsteini* (Vologdin) S (Ar)
 TN2 *Archaeocycyathus cumfundus* (Vologdin) S (Ar)
38. Malyy Aim River, Siberian Platform, Russia.
 Age: TN2, '*grandiperforatus*' Zone
 TN2 *Archaeocycyathus okulitchi* (Zhuravleva) (Ar)